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Behavior of Vatesus Beetles Associated with Army Ants (Coleoptera: Staphylinidae)¹

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In previous papers on staphylinid guests associated with army ants (Akre and Rettenmeyer, 1966), guests were separated into categories on the basis of their trail-following behavior and degree of host association. *Vatesus* were placed into the group having the closest possible relations with their host. Since then, more data has been obtained on the behavior of *Vatesus* beetles and is reported.

The tribe Vatesini contains only one genus and more than 25 species (Seevers 1965). All members are limulodid (horseshoe crab-shaped) in form, but differ from other Trachyporines in that they are associated with army ants. Discussion in this paper will be limited to the behavior of 3 species of *Vatesus* on which both field and laboratory data were collected.

Akre and Rettenmeyer (1966), in the first behavioral paper on staphylinids associated with army ants, discussed the behavior of the Aleocharinae, Paederinae, and Staphylininae, but omitted the Vatesini. The report also contained methods used in studying army ants and their guests.

Rettenmeyer (1961) includes an excellent discussion and much information on 6 species of *Vatesus* he collected with army ants in the

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Canal Zone. Other than this report, all other papers on *Vatesus* are primarily taxonomic and give at most only host data.

This report was part of a study made in Panama during 1963, 1967, and 1968 at the Smithsonian Tropical Research Institute, Canal Zone.

VATESUS CLYPEATUS (Wasmann) Species Complex

Although Borgmeier (1961) included V. clypeatus and V. gigas as separate species in his key to Vatesus, Seevers (1965) considered V. clypeatus, V. gigas, and V. panamensis as a species complex since he could find no means of differentiating them. The antennal characters given by Borgmeier do not hold true for large samples.

Rettenmeyer (1961) stated there was some doubt as to the taxonomic status of V. panamensis and V. clypeatus, but included his data on the Vatesus clypeatus complex by using V. panamensis as the species name since Barro Colorado Island was the species locality for V. panamensis. While all our specimens were collected on Barro Colorado, we prefer to use the species designation V. clypeatus to refer to this complex until taxonomic difficulties are resolved.

Rettenmeyer (1961) collected 59 V. clypeatus (= panamensis) with Eciton burchelli (Westwood), E. hamatum (Fabricius), E. vagans (Oliver), E. dulcius crassinode Borgmeier, and possibly E. mexicanum Roger. We collected 189 adult V. clypeatus from the following hosts: 16 colonies of E. burchelli (39), 24 colonies of E. hamatum (136), one colony of E. dulcius crassinode (5), and 3 colonies of E. vagans (9). In addition, 7 colonies of E. burchelli, 4 colonies of E. hamatum, 3 colonies of E. dulcius crassinode, 3 colonies of E. vagans, and 4 colonies of E. mexicanum had none. If V. clypeatus is found with E. mexicanum, it must be quite rare. All but 2 of the beetles were collected from emigration columns. One of these 2 beetles was collected in a refuse deposit column and the other was collected while digging out a subterranean bivouac of E. dulcius crassinode.

We found Vatesus clypeatus in emigration columns only when brood was being carried (Fig. 6). They usually appeared after brood had been carried for about 20 minutes and ant traffic was heavy. A few Vatesus were collected after the queen had passed and the emigration was nearly over. Only one Vatesus was collected at the end of the emigration after all the ants had passed, and it appeared slightly injured. The inquilines always ran in the center of the column. They were never seen to deviate from the trail like other guests such as the staphylinid Tetradonia marginalis Reichensperger (Akre and Rettenmeyer, 1968). None was ob-

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served riding on the ants or brood. Whenever an emigration column was disrupted by collecting, the ants would pile the booty and brood in clusters under leaves or in concealed crevices. *Vatesus* were observed buried in these piles of brood at least 8 times. During these periods the beetles were ignored by the ants.

Vatesus spp. have functional wings and have been collected in quantity at light (Borgmeier 1961). Although we ran ultraviolet and incandescent lights and a malaise trap for a total of 8 months, no Vatesus clypeatus was collected. While this beetle has functional wings, all 180 specimens examined had these wings broken off at lines of weakness anterior to the distal margins of the elytra.

Experiments revealed the antennae of V. *clypeatus* are the sites of trail chemoreception. Chemical trails were made using the methods given by Akre (1964), and such trails were tested with unmodified beetles as well as ones that had suspect chemosensory appendages removed. Ether had no effect on trail following ability since control specimens readily detected a trail as soon as they recovered from the anesthesia, so this anesthetic was used to permit removal of appendages.

The antennae of V. clypeatus are 11 segmented; a long scape, short pedicle, and a 9 segmented flagellum. Removal of both flagella resulted in cessation of all movement. With one flagellum removed specimens were very active and readily followed a trail. Lateral movements from one side of the trail to the other, compensating for the loss of one appendage, were exaggerated and suggestive of klinotactic orientation. The successive removal of flagellomeres revealed that speciments were able to sense a trail with 2 flagellomeres remaining on each antenna. None of 4 specimens with only the basal flagellomere were able to sense a trail, but 3 specimens with the 2 basal flagellomeres readily followed a trail 12–24 hours after amputation.

When following a trail *Vatesus* exhibits rapid lateral antennal movements, but the antennae do not appear to touch the substrate. Distinct trichoid sensillae are located on the flagellomeres; several on the terminal segment and 3 on the distilateral margin of each remaining flagellomere. These hairs are probably the site of chemoreception.

The possession of chemosensory ability on nearly all flagellomeres would seem to be of distinct advantage if specimens frequently lose parts of their antennae from being attacked by the ants. However, examination of many specimens did not reveal missing flagellomeres as is frequently found in the myrmecophilous thysanuran, *Trichatelura manni* (Caudell). Three Vatesus adults were kept alive in laboratory nests with their host ants for 22 days in 1963 and 12 Vatesus were kept alive for periods of 10–15 days in 1967 and 1968, other V. clypeatus were kept alive for shorter periods. During these times the Vatesus were observed through a broad field binocular microscope at least one hour daily.

The ants under observation were fed booty and brood from other army ant colonies. The beetles were frequently observed feeding on this food. While they were able to chew holes in dead army ant brood with great difficulty, they were usually unable to cut holes in booty without an assist from the ants. Four Vatesus had been in a nest without food for one day when some wasp (Polybiinae) larvae were placed in the nest. The staphylinids immediately crawled on top of the larvae and the mouth parts of the beetles moved every rapidly over the surface of the larvae (strigulation). Several tried to chew the larvae, but no beetle was seen to cut a hole in the tough and pliable integument. The Vatesus were constantly chased by the ants also feeding upon the larvae. Other Vatesus ate dead E. hamatum, E. burchelli, E. vagans, E. dulcius crassinode, and E. mexicanum brood. The adult Vatesus were never seen killing live brood as has been observed with other myrmecophiles (Akre and Rettenmeyer, 1966; Akre, 1968). More frequently than eating the brood themselves, Vatesus fed on juices oozing from holes cut in the larvae by the ants or by other guests such as histerids. Frequently the beetles attempted to feed on the brood while the ants were feeding but were always chased away. The ants were extremely intolerant of Vatesus and frequently attacked them. When the workers first chased Vatesus, the beetles took a very zigzag course and usually lost the attackers. If the workers chased them farther than a few centimeters, the inquilines dug down in the soil of the nest until only the tops of their pronota and elytra were exposed. Although the ants bit at the beetles, they were unable to grasp their smooth top surfaces and quit shortly.

In nests, the *Vatesus* spent most of the time near the brood, or near booty that was supplied as food. The ants always made a compact pile of the brood and then clustered on top of it. The staphylinids frequently buried themselves in the pile of brood or dug down in the soil under the pile, remaining there for hours. It was assumed they were feeding, but this was not observed; alternatively they might associate with brood to receive booty or to ensure a colony would not leave without them. The *Vatesus* were frequently attacked by ants standing on the brood as they ran between the ants' legs. However, only one *Vatesus* was seen killed by the ants. This staphylinid appeared moribund and an ant grasped one of its legs and turned it over. The workers soon cut off all the inquiline's legs, rendering it helpless. The next day only bits of the pronotum and elytra could be located.

The *Vatesus* spent many hours in the laboratory nests buried under the soil with only the tops of their pronota and elytra exposed. In this position they were impervious to attack by the ants. However, when a worker passed a partially buried *Vatesus*, it sometimes sensed the beetle and began to dig frantically in the soil. Soon nearby workers began digging, probably in response to alarm pheromone. If the digging got too close, the *Vatesus* scurried away and dug down in another location.

LIFE CYCLE

Rettenmeyer (1961) reported the first collections and identification of $Vatesus \ clypeatus \ (panamensis)$ larvae (Fig. 1) from 2 colonies of E. hamatum and one colony of E. dulcius crassinode. The latter may not have been V. clypeatus as Vatesus goianus Borgmeier is also associated with crassinode.

Table 1 lists data for 200 larvae of Vatesus clypeatus collected from 2 colonies of E. burchelli (9), 8 colonies of E. hamatum (167), and one colony of E. vagans (24). Rettenmeyer (1961) collected nearly all his larvae (over 70) at or near the end of the emigrations. We collected 48 larvae from various colonies after all the ants had passed or at least when ant traffic was sparse at the end of emigrations. All the remaining larvae (except 8 collected in refuse deposits) were collected throughout the emigration after brood was being carried, with no larvae passing after all the ants were gone. The entire emigration was observed for all colonies listed in Table 1 except Ec-151, E. vagans, where we observed only the last 20 minutes.

Table 1 also shows the sex of most of the adults collected in these colonies. Although some adults may have left the colony or died when the colony was in statary, this total represents all adult *Vatesus* in the colony when we watched it. However, one colony was not observed during the entire emigration. Colony Ec-115 had 54 larvae but only one adult female *Vatesus*. Other collections listed in Table 1 also indicate that only a few females must have laid all the eggs.

Larvae collected in emigrations ran either in the center of the column with ants running over and around them, in the center of the column with frequent deviations to the edge, or on the edge of the column out of the ants' way. Many stopped and hid under leaves or in crevices if there was any disturbance of the column. In marked contrast to their behavior



FIG. 1. Larval Vatesus, mature and ready to pupate. FIG. 2. Prepupa. FIG. 3. An older prepupa starting to pupate with the abdomen already emerging from the prepupal integument. FIG. 4. Pupa that was unable to shed the larval integument. FIG. 5. Pupa. FIG. 6. Vatesus adult in emigration column of *Ection hamatum*.

under laboratory conditions, the ants paid no attention to the larvae regardless of their position in the column. It was evident from observing OCTOBER 1969] AKRE & TORGERSON—VATESUS BEHAVIOR

	Adults					Nomadic-Statary	
Colony #	Species	Male	Female	Total	Larvae	Collected	Day
E -321	E. hamatum	?	4	6	12	end of emig.	lst. nomadic
Ec- 13	E. burchelli	2	1	8	7	end of emig.	4th. nomadic
Ec- 85	E. hamatum			?	3	refuse deposit	Statary
Ec-111	E. hamatum	5	3	8	29	5 refuse de- posit, rest scattered	lst. nomadic
Ec-115	E. hamatum	5	1	6	54	Scattered	lst. nomadic
Ec-122	E. hamatum	. 4	3	7	22	Scattered throughout	lst. nomadic
Ec-134	E. burchelli	?	?	2	2	end of emig.	lst. nomadic
Ec-141	E. hamatum	1	?	2	8	Scattered 5, 3 at end of emig.	lst. nomadic
Ec-146	E. hamatum	6	7	13	36	Scattered	lst. nomadic
Ec-151	E. vagans	4	1	5	24	end of emig.	Prob. 2 or 3rd nomadic
Ec-166	E. hamatum	ı 3	5	8	3	Scattered	Prob. 3 or 4th. nomadic

TABLE 1. Vatesus clypeatus collected with Colonies.

larvae found at the end of emigrations that they sense and use the chemical trails of the ants as do the adult *Vatesus* (Rettenmeyer, 1961; Akre and Rettenmeyer, 1968).

Adult *Vatesus* are extremely good trail followers, making them ideal for bioassaying the length of duration of trails in the field. Specimens were released on host trails 12–24 hours following their collection. During the intervening time they were without host contact.

Fourteen specimens were released a total of 8 times on host trails, but only once did a specimen appear to sense the trail or follow it for any distance. The morning subsequent to the emigration of colony Ec-2, *E. hamatum*, a specimen was released near the old bivouac site and continuously observed for 2.25 hours. During this time it moved 17 m along the emigration trail. Little difficulty was encountered when the specimen moved on roots or lianas, but in leaf litter or at points where the ants had formed an emigration bridge the specimen encountered considerable difficulty sensing the trail.

A Vatesus released on the emigration trail of Ec-11, *E. humatum*, less than 48 hours after the ants moved, chose to follow a trail freshly laid by 50–100 ants released a few hours earlier, rather than the emigration trail which at times was 5–7 ants wide.

Whether specimens were released in darkness or during the day seemed to have no effect. A Vatesus released on an E. burchelli trail, about 16 hours after the ants had moved, was observed for one hour with red light. During this period it seemed to be following the trail about 10% of the time. In one hour it moved 178 cm from the release point. It explored all roots and lianas lying in the path of the emigration route, following those routes which most readily facilitated its passage even though these features were not part of the emigration route.

Twenty minutes after the last ant of colony Ec-141 (*E. hamatum*) emigrated, a *Vatesus* was released 2.5 m from the old bivouac. Within 10 minutes the specimen covered 20 m of trail over large lianas and leaf litter. We could detect no difference in the specimen's ability to sense this quite fresh trail on either surface. This same specimen was released at the identical location 10.5 hours later, but gave no indication of ability to follow the trail. A similar procedure was repeated after the emigration of Ec-159, *E. hamatum*. Upon release the specimen initially moved toward the old bivouac 4 times. Each time it was re-aspirated for fear of losing it. The fourth time it moved 4.74 m in 3 minutes, in the direction of the emigration appearing to have little difficulty sensing the trail.

From these observations we conclude that only very fresh trails can be used by *Vatesus* in host finding. That trail following on old trails is not a method of host finding is further substantiated by Schneirla's observations (1933) that ant trails lack polarity.

Our collections indicate Vatesus lays eggs and the larvae develop during the host's statary phase. As mentioned above, we collected 8 larvae from the refuse deposits of E. hamatum; three from colony Ec-85, 14 days after we had located the colony which was in statary at that time, and the other 5 larvae from refuse deposits of Ec-111 the day before it became nomadic. In all cases the larvae were collected 10–50 cm from the base of the bivouac, running among the discarded cocoons and booty refuse. However, the larvae probably do not pupate in this location. We excavated 4 bivouac sites of statary colonies immediately after the ants became nomadic. All soil and debris around the bivouac site and to a depth of 10 cm was removed and placed in plastic bags. This was brought back to the laboratory and searched very carefully without finding any *Vatesus* larvae or pupae, indicating the larvae leave with the ants on the first nomadic day.

Larvae of various sizes and developmental stages were found in all colonies investigated indicating adults do not lay their eggs at the same



FIG. 7. Head capsule widths of 154 Vatesus larvae.

time or else one adult lays her eggs over an extended period of time. Alternate explanations could include differential embryonic development or larval growth. Figure 7 shows the head capsule widths of 154 larvae fall into 3 major groups so that at least 3 instars are present. However, the head capsule growth may slow down in later instars (Ludwig and Abercrombie, 1940) and head measurement is not recommended for determining instars because some instars may be left out (Gaines and Campbell, 1935). Since at least some staphylinids have only 3 instars, this indicates we may have collected all larval stages (Paulian, 1941).

An attempt was made to rear the larvae to maturity by placing them in round plastic containers, 15 cm diameter, with saran screen lids and plaster of Paris/charcoal bottoms. Sterile soil (heated for 30 minutes) was placed over the plaster to a depth of ca 1 cm. No ants were placed in these boxes because the ants always killed the larvae. Larvae were fed army ant brood, live phorid maggots, and another myrmecophile, the thysanuran, Trichatelura manni (Caudell). Most of the larvae did not feed, and either changed into prepupae or died. However, a few were voracious. Four larvae, placed in a box with E. hamatum brood, began to feed immediately. Although the brood was still alive, one beetle larva devoured 3 small ant larvae in rapid succession. In several days nearly all the brood (about 50 small larvae) had disappeared and was assumed eaten. Several other larvae fed on dead brood of various army ants, but the larvae seemed to prefer to kill and eat T. manni. This silverfish was their most readily accepted food. The integument of the silverfish is quite soft and the larvae readily killed and ate even the largest individuals. However, the larvae had difficulty catching T. manni unless

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both were placed in small containers. Therefore, the *T. manni* were injured before being placed in the 15 cm containers to facilitate feeding. Anywhere from 3-10 larvae were placed in each container. A total of 79 were retained in this manner. Eleven of the larvae changed to prepupae within 4-11 days after their collection and 3 pupated within 5-8 days. Most of the remaining larvae died within 6-7 days but 4 were still alive and active 16 days after their capture.

Before changing into prepupae, the larvae dug into the soil and made an earthen cell where they became quiet. The prepupae are described by Rettenmeyer (1961) as curved with the head and legs drawn close together (Figs. 2, 3). He also stated that no movement could be detected in the prepupae when they were handled with forceps. However, all prepupae we handled exhibited characteristic pupal movements and any that failed to move were usually dead or dying. Although the larvae changed into prepupae beneath the soil, the soil in our laboratory nests was not deep enough or was of incorrect texture because the movements of the prepupae uncovered most of them before they pupated and may have contributed to their death.

Only 3 of our larvae pupated. One of these, under the soil in an earthen cell, managed to cast off the prepupal skin completely. The other two prepupae were on the top of the soil and died without completely shedding the larval skin (Fig. 4). The first pupa was subsequently killed by a predaceous mite and none of the pupae completed development. Of these 3 pupae, 2 lived for 10 days in the pupal stage. Whether the pupal stage normally lasts this long is not known, but even if it lasted for only a few days the ants would leave the *Vatesus* behind.

We have only one record of a colony from which we collected larvae still following the emigration on the fourth nomadic day. In this instance only 7 larvae were collected. It appears that the *Vatesus* larvae probably follow the ants with a few larvae dropping out of the column and pupating each day.

The pupa that was able to completely free itself from the larval skin is shown in Fig. 5. Careful examination of the 3 pupae revealed fully formed secondary wings. Since all adult beetles examined had the wings broken off, it seems likely that the newly hatched *Vatesus* fly to their host ants and then lose the tips of their wings.

VATESUS GOIANUS Borgmeier

Although V. goianus was reported previously only from Brazil with E. dulcius, we collected 3 specimens from an emigration column of E.

dulcius crassinode on Barro Colorado Island that fit the description of V. goianus well, and Seevers (Chicago) indicated they probably were that species. In addition to the 3 adult V. goianus, 5 larval Vatesus were collected at the end of the emigration after all the ants had passed. Since both Vatesus clypeatus and V. goianus occur with E. dulcius crassinode, the larvae may have been of either species. However, since the entire emigration was watched and no adult V. clypeatus were collected; it is probable the larvae are V. goianus. The larvae have not been examined to reveal differences.

The behavior of adult V. goianus was similar to V. clypeatus in the field and laboratory. The adults were picked out of the center of the emigration column when brood was being carried. In laboratory nests these staphylinids fed on the brood and booty provided the ants as food, but spent most of their time in the nests partially buried in the soil.

All these V. goianus had lost the tips of their wings along lines of weakness just like V. clypeatus.

VATESUS PRAEDATORIUS Seevers

Seevers (1958) description and illustrations of V. praedatorius are in error and identification cannot be made from his paper. Type specimens were borrowed from the Snow Entomological Museum and identification was made by using these specimens.

Twenty V. praedatorius were collected in a raid column of Labidus praedator (F. Smith) on 26 June 1968. The raid column was found at 8:40 p.m. and at that time was 10–12 ants wide. All the ants were apparently returning to the bivouac with booty. The column emerged from a hole in the ground, moved over the top of the soil for about 3 meters, and then disappeared into another hole in the ground. The column was observed from 8:40-11:30 p.m. when it ceased abruptly. One moment it was 10 ants wide and suddenly there were none. The Vatesus were collected throughout this time running in the center of the column and 2 were collected at the very end after the ants had passed. One Vatesus was collected riding on the posterior end of a piece of booty carried by an intermediate worker.

Upon returning to the laboratory, the *Vatesus* were placed in a laboratory nest with their host ants. Eighteen were kept alive for 6 days, and the remaining 2 for 11 days before preservation. During the period they were kept in the laboratory, observations were made on their behavior for at least 2 hours daily.

The behavior of V. praedatorius was also similar to that of V. cly-

peatus. However, these small Vatesus seemed to be constantly active in the nests and ran from one cluster of ants to another. If any did remain still they were on the top of the soil or in the tunnels dug by the ants. They did not bury themselves as did V. clypeatus.

The Vatesus were very active, feeding on booty collected along with the ants and on dead E. hamatum brood furnished the ants as food. Although the beetles were observed feeding many times, we could not determine if they actually chewed holes in the brood and booty. The mouth parts of the beetles strigulated over the surface of the food, and several times the beetles were seen chewing with their mandibles on booty and brood. However, the mandibles appeared to be quite inefficient and the beetles seemed to feed more on the juices and materials oozing out of the holes cut by the ants.

The host ants constantly attacked and chased V. praedatorius but were never seen to be successful in capturing or killing a specimen.

All 20 specimens of V. praedatorius had functional secondary wings and could probably fly, although none attempted to fly even when dropped.

DISCUSSION

These three species of *Vatesus* are closely integrated with their respective host army ants. Even though they are attacked constantly in the unnatural situation present in a laboratory nest, the beetles always remained close to the ant cluster and brood. All have the ability to use fresh chemical trails laid by the army ants.

All 3 species are predaceous on army ant brood but in nature they probably feed entirely upon the booty brought in by the ants. In either situation they are heavily dependent upon the ants both to furnish the food and to tear it open so it is readily available.

Although Vatesus are good trail followers (Akre and Rettenmeyer, 1968), our observations indicate that adults apparently fly to their host ants. All specimens of Vatesus clypeatus and V. goianus collected in the field had their wings broken off along fold lines and could not fly. However, several pupae of V. clypeatus had fully developed wings indicating that freshly emerged individuals have functional wings. These wings must be broken off sometime after the Vatesus locate their host ants. A similar case occurs in the Heleomyzidae (Diptera). The type series of Lutomyia hemiptera (Curran) have all but the basal portion of the wing torn off (Gill, 1962). This mutilation of the wings apparently occurs after the flies locate the rodent burrows in which they live. The adult Vatesus lay eggs during the statary phase of the ants' cycle. When the

ants emigrate the nearly grown larvae move with the ants until they pupate. Since Vatesus are excellent trail followers they should have no difficulty in locating their host by species odor; especially Vatesus clypeatus that has several host species. V. goianus probably flies to find its host since E. dulcius crassinode seems to have regular periods of no-madic-statary phases as E. hamatum and E. burchelli. Labidus praedator does not seem to have regular cycles and V. praedatorius may be able to complete its development without being left behind by the ants. However, it has functional wings at all times and should be able to locate its host ants readily if it cannot complete its development while the ants are statary.

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